Morphological and behavioural evidence of relationships of the Cuckoo Finch *Anomalospiza imberbis*

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Viduids are African finches that are obligate brood parasites, using other species to incubate their eggs and care for their young (Payne 1996, 1997a, b, 1998). Of 20 viduid species, 19 are indigobirds and whydahs in the genus *Vidua*, and one is the Cuckoo Finch *Anomalospiza imberbis*. Recent analysis of mtDNA sequence data supports the idea that *Anomalospiza* and *Vidua* are each others' closest relatives and their common ancestor was a brood parasite (Sorenson & Payne 2001). The molecular genetic distance between the two genera indicates that brood parasitism originated in these finches *c*. 17-20 million years ago. Moreover, the parasitic finches (Viduidae) are most closely related to the grassfinches (Estrildidae) in a sister relationship, and are not closely related to the weaverfinches (Ploceidae) (Sorenson & Payne 2001).

Anomalospiza are yellowish in plumage (adult males in breeding season; they are more dull in the non-breeding season) or sparrowy-brown (females and juveniles), stocky, thick-billed birds. They superficially resemble in plumage a number of other finches with which they flock in the breeding season. They are brood parasites on *Prinia* and *Cisticola* warblers of open grasslands (Vernon 1964).

The systematic relationship of *Anomalospiza* has a long and contentious history. Although no comprehensive phylogenetic analysis included *Anomalospiza* until Sorenson & Payne (1998, 2001), certain morphological and behavioural features had been used to support its affinity with various families. Here we describe morphological and behavioural features which support the molecular evidence that *Anomalospiza* is a viduid finch.

Taxonomic history

The Cuckoo Finch was originally described as a canary (*Crithagra imberbis*, Carduelinae; Cabanis 1868); Sharpe (1888) included it in another canary genus *Serinus* in the family Fringillidae, and Reichenow (1904) also considered it to be a canary. Other Old World finches were placed in a broadly conceived Ploceidae (Sharpe 1889). Shelley (1901) described the genus *Anomalospiza* based on the deep, compressed bill, straight edge of the culmen, and the uniquely angled shape of the cutting edge of the lower mandible, and recognized the bird as related to the weaverbirds Ploceidae, in his subfamily Viduinae (Shelley 1905). This was based on wing shape, with short outer primary and plumage dimorphism like that of *Euplectes* and *Quelea*, along with *Vidua* (Shelley 1905).

Chapin (1917) provisionally placed *Anomalospiza* in his Estrildinae, which included Shelley's Viduinae, based on the bill shape and tenth primary size, which are similar to Locust Finch *Paludipasser locustella*. Chapin envisioned that a study of *Anomalospiza*'s nest and nestlings would someday resolve the issue. Meanwhile, field research suggested (Roberts 1913), then confirmed (Roberts 1917, van Someren 1918), that *Anomalospiza* is a brood parasite; moreover, further study revealed that it is obligate in that occupation and it builds no nest (Roberts 1939, Friedmann 1960). Delacour (1943) removed *Vidua* and *Anomalospiza* from Estrildinae, but did not keep the two genera together. *Anomalospiza*, he asserted, "is nothing but a Ploceine weaver", a claim that he supported with plumage characteristics; whereas *Vidua* was grouped with *Euplectes*, in so doing combining the whydahs with widowbirds as "widows" ("veuves") (Delacour & Edmond-Blanc 1933-1934). Chapin (1954) guessed that nestling *Anomalospiza* had no mouth spots or papillae and reaffirmed his faith in its status in Ploceinae. Nearly all later systematists recognized *Anomalospiza* as a ploceid rather than an estrildid or viduid, and Friedmann (1960) thought it "is clearly not closely related to the Viduinae". However, Bannerman (1949) placed *Anomalospiza* in Viduinae because its short strong bill and minute tenth primary were unlike typical ploceine weavers.

Williams & Keith (1962), in the light of Chapin's (1954) observation that adult males had incompletely pneumatized skulls, provided more specific data regarding this condition, and noted this as a viduid feature (as in White 1948), although a few other birds such as crossbills *Loxia* and Darwin's finches *Geospiza* also have unpneumatized skulls in the adult. Finally, Benson & Pitman (1964) discovered information which had been awaited for half a century, that *Anomalospiza* nestlings do not have the mouth markings of the *Vidua* parasitic finches. Vernon (1964) claimed the lack of mouth markings and the shape of the nestling bill to be evidence of a ploceid relationship. Nicolai (1964), however, recommended that adaptive characters such as the mouth markings of the young should not be used to infer phylogenetic relationships of the parasitic finches. In the field, Vernon (1964) found that female *Anomalospiza* generally remove all eggs from the host's nest when she lays her own, whereas female *Vidua* occasionally remove a host egg but leave the others in the nest (Morel 1973). Hall & Moreau (1970) doubted the utility of behavioural data in determining the systematic status of *Anomalospiza*, however, since the parasite could have diverged from its closest relative. Morlion (1971, 1980) did not include *Anomalospiza* in her study of the pterylosis of African finches. Bentz (1979) found that *Anomalospiza* had, like other Old World finches, an undiagnostic forelimb myology, and a hindlimb myology like certain ploceids. Biochemical tests of birds in the Ploceidae-Estrildidae assemblage (Sibley 1970, Kakizawa & Watada 1985, Christidis 1987, Sibley & Ahlquist 1990) did not include samples of *Anomalospiza*. Payne (1997a,b) and Sorenson & Payne (2001) recognized Viduidae (whydahs and indigobirds, together with Cuckoo Finch), Estrildidae (waxbills) and Ploceidae (weavers) as separate families, and this nomenclature is used throughout the present work.

Morphology

Specimens of *Anomalospiza* in the University of Michigan Museum of Zoology (UMMZ) were examined, including 15 skins, seven skeletons and four alcohol specimens, and additional alcohol specimens were examined at the American Museum of Natural History (AMNH) in New York and the Natural History Museum (NHM), Tring.

Pterylosis

The families Ploceidae, Viduidae and Estrildidae were distinguished from a more broadly conceived family Ploceidae of Sharpe (1889) on the basis of the length and shape of the outermost (tenth) primary (Shelley 1905, Chapin 1917). Ploceids in the more restricted sense in fact range from having from a large tenth primary (malimbes *Malimbus*) to a nearly nine-primaried wing (social-weavers *Pseudonigrita*). Bannerman (1949) indicated that the minute or vestigial outer primary in *Anomalospiza* was more like that of Viduidae and Estrildidae than of Ploceidae. Chapin (1917) rejected the character as an important basis for systematic inference because "it does not express real relationship" and "there are numerous exceptions"; *Quelea*, for instance, is close to *Vidua* on this basis but not in other characters examined. Sushkin (1927) claimed that the tenth primary was "declining" in these birds and therefore should not be used as a taxonomic criterion. Delacour (1943) and Moreau (1960) denied the usefulness of tail or wing lengths, particularly the tenth primary, in determining family status in the finches.

To compare the feather structure and feather tracts of Old World finches, Morlion (1971, 1980) examined 21 ploceids, four *Vidua* and 15 estrildid finches, but not *Anomalospiza*. We compared skins and alcohol specimens of *Anomalospiza* with Morlion's results for Ploceidae, *Vidua* and Estrildidae, where these characteristics were consistent within a family and were visible in the specimens examined. Several morphological features are similar in *Anomalospiza* and *Vidua*. *Anomalospiza* has a short, narrow outer primary as in *Vidua* and Estrildidae (although this primary is long in the estrildid twinspots *Clytospiza* and *Euschistospiza* and bluebills *Spermophaga*); it is large in most Ploceidae, though it is short in *Euplectes* and *Quelea*. *Anomalospiza* shares with *Vidua* several features of the feather tracts that are unlike ploceids, estrildids or either of these, or that are like estrildids but not ploceids: (1) 2 rows of upper greater secondary coverts, (2) 8 upper median secondary coverts (as also in Estrildidae), (3) 4 upper tertiary coverts (as also in Estrildidae), (4) 9 under greater primary coverts, (5) 1 row of ocular feathers (as also in Estrildidae), (6) 8 longitudinal rows of feathers on the crown, and (7) 3 rictal bristles (as also in Estrildidae). In these seven characters the pterylosis of *Anomalospiza* resembles that of *Vidua* rather than Ploceidae. In the number of under lesser primary coverts, however, *Anomalospiza* has a minute tenth covert; *Vidua* lack a feather in this position, and Ploceidae have a full-sized tenth covert. *Anomalospiza* share no features of the feather tracts with ploceids that differ from *Vidua* and the estrildids.

The many similarities of pterylosis in *Anomalospiza* and *Vidua*, and the differences between these forms and other Old World finches, indicate that the similarities are synapomorphies, shared traits that evolved in the common ancestor of these two genera.

Plumage

Delacour (1943) believed *Anomalospiza* to be a ploceid because males are sparrowy-brown in the nonbreeding season and look like females, and van Someren (1922) thought there were two moults of plumage in a year, but in fact male *Anomalospiza* are yellowish below in all seasons and do not have a sparrowy-brown female-like plumage once they have moulted from the juvenile plumage. Males are streaked greenish and black above in all seasons but are brighter above and brighter yellow below in the breeding season. Friedmann (1960) noted the similarity between female plumage of *Anomalospiza* and that of the ploceid *Euplectes.* Nicolai (1964) noted that the other viduids are similar to the ploceids with respect to a seasonal alternation of male breeding and nonbreeding plumage. *Anomalospiza* and *Vidua* differ in the manner in which the breeding plumage is acquired. In *Vidua,* males moult into their breeding plumage, but in *Anomalospiza* the cryptic tips of the feathers wear off to reveal the brighter yellow breeding plumage (Bannerman 1949). The plumage colour and pattern of *Anomalospiza* lacks obvious synapomorphies that are unique to one of these families of finches.

Cranial skeleton

Viduid finches, unlike most passerine birds, have a peculiar delayed ossification of the dorsal region of the adult skull, in which the frontal region of the skull consists in part of a single, unpneumatized layer of bone, much as in juveniles of other songbirds (Chapin 1917, White 1948). Chapin (1954) described an adult *Anomalospiza* with an incompletely pneumatized skull, and Williams & Keith (1962) found only one of 14 adult *Anomalospiza* with a fully pneumatized skull; in the other specimens, 10 to 30 % of the skull was unpneumatized. In the UMMZ *Anomalospiza*, 13 of 15 adult specimens (including all six laying females with an egg in the oviduct or with recently ovulated follicles) with skull data were incompletely pneumatized. Another bird was captured as an adult and was kept in an aviary, and three years later it had a fully pneumatized skull. In Village Indigobirds *Vidua chalybeata* a few birds taken in the field were fully pneumatized, and in captivity the birds sometimes completed their skull pneumatization within four years (UMMZ, RBP). The incompletely pneumatized skull and its delayed maturation in adult *Anomalospiza* and *Vidua* indicate developmental synapomorphy from a common ancestor.

In *Anomalospiza* the bill is short and stout; the jaw is bent downward at the frontal-nasal-maxillary hinge at an angle of *c.* 110° relative to the jugal, and the jugal has a laterally compressed expansion and ventral protuberance.

Several characteristics of the bony palate differ between the Ploceidae and *Vidua*, although they were not utilized in the historical debate over *Anomalospiza.* Sushkin (1927) suggested the width of the palatine crests differed between ploceids and viduids. The difference is inconspicuous; although *Anomalospiza* resembles *Vidua* it also is similar to the ploceid *Quelea*. Sushkin also suggested that the shape of the vomer differs between Ploceidae and Viduidae; however, the vomer of *Quelea* is similar to *Vidua*, being cup-shaped. *Anomalospiza* is like an extreme *Vidua* in this respect, the vomer having a deep curling concavity. The parasphenoid rostrum and the nasal were the most consistent characters mentioned by Sushkin as differing between Ploceidae and Viduidae. In both cases the differences are distinct, and in both characters *Anomalospiza* is like *Vidua*. Examination of specimens in UMMZ shows a few additional characters. The medial region of the premaxilla in Ploceidae is ridged (Village Weaver *Ploceus cucullatus*, Red-billed Quelea *Quelea quelea*) or flat (White-billed Buffalo Weaver *Bubalornis albirostris*), but in *Vidua* it is grooved and in *Anomalospiza* there is a very deep median groove. In addition, the pterygoids of *Anomalospiza* differ from both ploceids and the viduids, *Anomalospiza* being broadly flattened and rotated ventrally nearly 80º (like a parrot, e.g. Cockatiel *Nymphicus novaehollandiae*) as they approach the palatines, rather than narrowly flattened as in Straw-tailed Whydah *Vidua fischeri* (*Vidua* also have an ventrally rotated pterygoid). The pterygoid of *Anomalospiza* is much more distinctive in form than that of some other thick-billed finches (the estrildid Black-bellied Seedcracker *Pyrenestes ostrinus*, the ploceid Grosbeak Weaver *Amblyospiza albifrons*, the cardueline Hawfinch *Coccothraustes coccothraustes*).

Inside the mouth of *Anomalospiza* is a thick lateral area that is continuous with a bony ventral protuberance of the jugal bone. This condition is unlike that of other thick-billed finches: Black-bellied Seedcracker and Grosbeak Weaver have a somewhat broadened jugal but these lack a prominence along the middle of the shaft, while Hawfinch has a thickened middle jugal. The thick maxilla of *Anomalospiza* reduces the buccal volume by more than half, to the size of a *c*. 3 x 2 x 2 mm seed. *Anomalospiza* has an extremely forceful bite for a bird of its size (Payne 1997b, pers. obs.). The bill breaks hard seeds and crushes them, as indicated by the shape of the horny palate as discussed below, by the thick, flattened lower mandible and by crushed seeds in the crop.

The thick bill of *Anomalospiza* has several associated unique skeletal features. The extent to which these features are developed in *Anomalospiza* is unparalleled in *Vidua* or in the Estrildidae and Ploceidae. The bill shape and supporting skeletal features appear to be autapomorphies within the genus *Anomalospiza*, and they indicate no recent common ancestry with thick-billed ploceids or thick-billed estrildids.

Bill, mouth and palate

The bill shape of *Anomalospiza* is similar to certain ploceids, such as *Quelea,* which have short bills. However both the horny and bony palates and the mandibles of

Anomalospiza are distinctive, and differ significantly from either *Vidua* or the ploceid weavers.

Sushkin's (1927) analysis suggested differences in the horny palate of the estrildids, viduids and ploceids, but he did not explicitly generalize about each of these larger groups. Nevertheless the horny palate distinguishes Ploceidae and Viduidae, as suggested by Sushkin's descriptions of five ploceids and one viduid species. Examination of UMMZ specimens of four additional ploceids (Grosbeak Weaver, Yellow-crowned Bishop *Euplectes afer*, Village Weaver, Red-billed Quelea) and two additional viduids (Village Indigobird *Vidua chalybeata*, Eastern Paradise Whydah *V. paradisaea*) corroborates the distinction. Ploceidae have lateral ridges in the palate that do not converge, or converge only in the far posterior region, with the median ridge unobstructed for nearly the entire length of the bill. *Amblyospiza* is an exception and has a more generally raised posterior portion of the palate that obscures all ridges. All ploceids, including *Amblyospiza,* differ from the Viduidae. Both *Anomalospiza* and *Vidua* have two large pits bilaterally, near the posterior of the palate. The pits displace the lateral ridges inward; the lateral ridges converge upon and obscure the median ridge, beginning from halfway to two-thirds along the bill and continuing posteriorly. These pits occlude two horny pads in the lower mandible. In *Vidua* a median ridge is present on the palate; in *Anomalospiza* a median ridge is absent, and the horny palate, except the pits, is greatly thickened for crushing hard seeds.

Chapin (1917) wished for a "rearrangement of the groups in accordance with the decorations, or lack of them, in the mouths of their nestlings". Nestling viduid and estrildid finches have mouth markings and gape papillae (Neunzig 1929a,b, Nicolai 1964) that are absent in nestling ploceid finches. Benson & Pitman (1964) and Vernon (1964) found *Anomalospiza* not to have such spots, and Vernon placed it in Ploceidae for this reason. The nestling hosts of *Anomalospiza* do not have gape and palate markings, whereas the nestling hosts of *Vidua* do. In *Vidua* the markings, like those of their host young, may function to elicit parental care from the foster parents (Payne *et al.* 2000, 2001), so the absence of gape and palate markings in *Anomalospiza* might be expected because their hosts have none. Most likely these nestling traits were lost when *Anomalospiza* split from *Vidua* (Sorenson & Payne 2001). In *Vidua* the gape and palate markings continued to evolve in mimicry, as indicated by the close match between each species of *Vidua* and its host species (Nicolai 1964, Payne 1997a,b).

Anomalospiza resemble *Vidua* in the unique pits on the horny palate. Other features of the bill and palate of *Anomalospiza* are uniquely derived, and no features indicate a close relationship with the thick-billed ploceids.

Postcranial skeleton

Chapin (1917) noted that Estrildidae and Viduidae do not differ from Ploceidae on the basis of postcranial skeletal characters, and that the White-billed Buffalo-Weaver *Bubalornis albirostris* has an anterior sternal spine and foramen complex that is unusual among passerines. Later, Chapin (1954) found a similar configuration in *Anomalospiza*. Examination of UMMZ skeletal specimens shows that *Anomalospiza* resembles Red-billed Buffalo Weaver *Bubalornis niger*, White-billed Buffalo Weaver and White-headed Buffalo Weaver *Dinemellia dinemelli*, and these differ from other passerines, in having a sternum with a large spina interna and the spina externa fused anteriorly into a laterally bifid tip, but separate posteriorly with a foramen near the dorsal base of the spinae sternale. This anterior sternal foramen is a medial extension of the sulcus carinae and it accommodates the angulus medialis of the coracoid, the bone that articulates with the sulcus carinae of the sternum. Other finches (*Vidua*, *Spermophaga*, *Amblyospiza*) have a large bifid spina externa as do most passerines, but these finches lack a spina interna dorsal to the sulcus carinae; the sulci barely meet dorsal to the spina externa, and they lack a medial foramen at the base of the complex. There are no other unusual skeletal features in which *Anomalospiza* resembles these two buffalo weaver genera, and their anterior sternum complex appears to have evolved independently in these birds.

Appendicular muscles

Bentz (1979) examined the appendicular myology of *Anomalospiza imberbis*, 10 species of ploceids, 28 estrildids and a viduid finch (Eastern Paradise Whydah). *Anomalospiza* was equally similar to the ploceids and *Vidua* in all five forelimb muscles and in four of six hindlimb muscles examined. One hindlimb muscle (M. obturatorius lateralis pars dorsalis) was small in *Anomalospiza*, variable in size in the ploceids, and absent in *Vidua*. M. iliotrochantericus medius was present in *Anomalospiza* and all ploceids, but absent in the *Vidua*. Only two muscles differed between *Anomalospiza* and the one *Vidua* species examined, and one of these was variable within Ploceidae. The appendicular muscles that have been examined do not provide useful information on finch phylogeny and more studies are needed.

Eggs

Viduids and estrildids lay unmarked white eggs, whereas the ploceids lay eggs of a variety of colours with a variety of spotting patterns (Friedmann 1960, Lahti & Lahti in press). Payne (1944) described an apparent *Anomalospiza* egg (he did not allow it to hatch), pink and purple with darker blotches and spots, unlike the bluer eggs of the host *Prinia*. Vernon (1964) compiled other observations of known *Anomalospiza* eggs which were similarly coloured to those of the hosts, and ranged from white to light blue, sometimes with speckles. If *Anomalospiza* eggs match those of their hosts, egg colour is not a useful phylogenetic character because it has been shaped by natural selection in association with brood parasitism. *Anomalospiza* and *Vidua* also have a larger clutch (number of eggs laid in a set, though usually not in a single nest) and smaller eggs relative to their body size than those of most ploceids (Payne 1977).

Behaviour

With the evolution of brood parasitism one expects significant divergence in behaviour, including those relating to courtship and mating. Even though behaviours may be secondarily derived in adaptation to brood parasitism (Friedmann 1960), such adaptations could arise more than once, so behaviours may be uninformative with respect to phylogenetic relationships. On the other hand, breeding behaviour could be uniquely derived within a clade, and consistent differences between the brood parasitic finches and the nesting finches in courtship displays and song behaviour may corroborate the molecular genetic results in determination of finch systematics.

The behaviours described below are consistent with the idea of a common origin of *Anomalospiza* and *Vidua*, but the behaviours are not unique to these birds, and some behaviours are adaptations to their brood parasitism of certain hosts.

Breeding display

The breeding display of male *Anomalospiza* differs from the aerial bobbing of most *Vidua*. *Anomalospiza* males display by fanning their wings at the female while perched (Williams & Keith 1962, pers. obs.) like many ploceid weavers (Crook 1958). However, Straw-tailed Whydahs display while perched in a similar manner (Nicolai 1969, Payne *et al.* 2002).

Egg removal

Friedmann (1960) remarked that *Vidua* egg removal from host nests exists "only to the extent of obviating what would otherwise be excessive crowding". Cheesman & Sclater (1935), however, suggested that *Anomalospiza* females regularly remove the host eggs, and generally only the parasite survives to leave the nest. Later, Vernon (1964) found that *Anomalospiza* does indeed remove all eggs in the host nest at the time of laying. *Vidua* females occasionally remove a host egg from the nest, but this is unusual in the field although common in captivity (Morel 1973, Payne *et al.* 2000, 2001). Unlike most other brood parasitic birds, *Vidua* chicks show no aggressive behaviour toward their nestmates, and the young in a parasitized nest usually fledge together with the host young and often with other young *Vidua* (Morel 1973, Payne *et al.* 2000, 2001). Usually the young *Anomalospiza* alone fledge in their host nest; although egg removal by the female is certainly a cause of this, the nestlings may trample or physically displace the host chicks as well (Friedmann 1960, Vernon 1964).

Feeding behaviour and foster parental care

Vidua feed on fallen grass seeds where they scratch the ground with both feet ("double scratch") nearly simultaneously to uncover seeds, hop backwards, then pick up the exposed seeds. Poulsen (1953) suggested that scratching during foraging is distinctive of Viduidae (in contrast to Ploceidae); the behaviour has been observed in most species of *Vidua* as well as in several New World Emberizidae (Greenlaw 1977). Although *Anomalospiza* feed on the ground, they have not been seen to double-scratch in the field, nor were captives that were observed for three years, even though they had sand in their aviary (RBP). Because the behaviour is common in two unrelated families and it occurs occasionally in other songbirds, it appears to have developed independently in *Vidua* and in other ground-foraging birds (Greenlaw 1977).

Vidua nestlings and fledglings feed by crouching, twisting the head and neck, waving the head from side to side and begging with the head upside down, like young of their foster estrildid hosts, whereas *Anomalospiza* young beg in an upright position without the head waving movements (Nicolai 1964, Friedmann 1960). The differences between *Anomalospiza* and *Vidua* in fostering behaviour involves a difference in nestling feeding. Young *Anomalospiza* receive insects from their foster parents held in the bill (*Cisticola* and *Prinia*) (Pakenham 1939, Benson & Pitman 1964, Vernon 1974), whereas young *Vidua* are fed seeds regurgitated by their estrildid foster parents (Nicolai 1964, Payne *et al.* 2001).

Vocalizations

The flight call of *Anomalospiza* was described by Vincent (1936) and Williams & Keith (1962) as a hard "jit-jit" or "cheet-cheet" and song as a high, chirping "choop-ee-choo" or a thin, sibilant "tissiwick" and "tissiway". Stevenson & Fanshawe (2002) described the flight call as a fast "titititit", and song as a "swi-sun-suit" with a weaver-like quality and sometimes with a long wheezy "vweeeeeooooo".

Songs were recorded at Lochinvar National Park, Zambia, in 1974, and at Belvedere marsh, Harare, Zimbabwe, in 1991 (Fig. 1). The song lasts about 4 s and

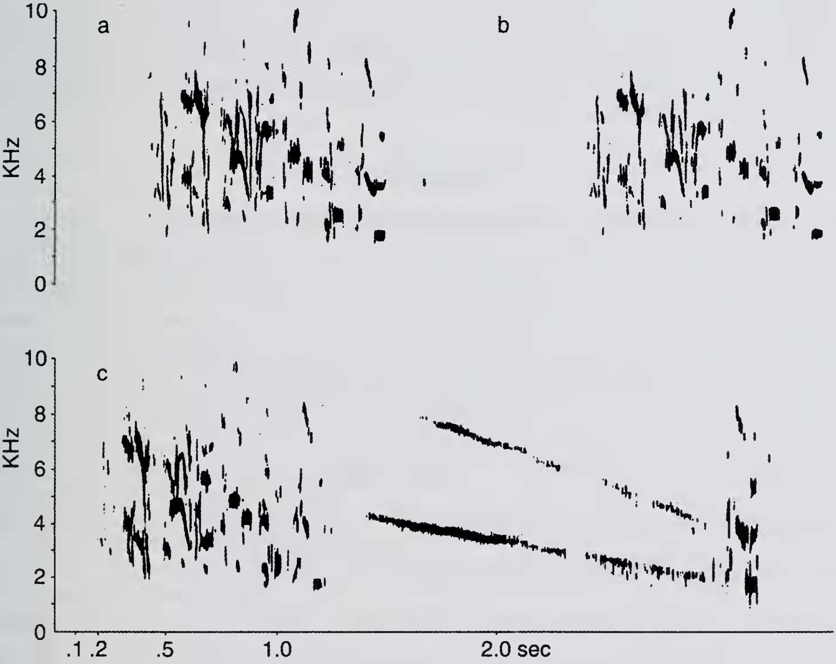

Figure 1. Audiospectrograms of songs of a male *Anomalospiza imberbis* at Lochinvar National Park, Zambia. a, b, short song; c, long song with whistle-buzz.

consists of three parts: (1) chirping notes are given in a repeated pattern, the series drops in pitch from 8 to 2 kHz and lasts 1.0-1.2 s. Each note type is given once, and ranges in length from 0.05-1.8 s; individual notes have a half-tone (a frequency trace occurs at half the pitch of the loudest trace) and most notes drop in pitch. This sequence is often given alone, and it is repeated almost exactly (Fig. 1). (2) a descending whistle-buzz "choo" or "vweeeeeooooo" is given, not as loud (by 10 dB) as the chirping series. This complex sound has a descending whistle with an upper trace beginning at 9 kHz and dropping to 4 kHz, a lower trace at half that frequency, and each trace with a descending buzz at half the frequency of the whistle; the whistle-buzz lasts 1.6 s. The whistle-buzz sounds like song-buzz of Village Weaver (Collias 2000) and the "kazoo" call of Dybowski's Twinspot *Euschistospiza dybowskii* (Payne & Payne 1995); (3) chirp at the end, with peak frequency the same as end of the whistle-buzz. Most songs included only the chirping series; three of 14 had the whistle-buzz. Songs in Zimbabwe were similar to those in Zambia though only in Zambia were the whistle-buzz elements recorded. These elements are of low amplitude, and the songs in Zambia were recorded at a distance of < 10 m. Unlike most *Vidua* species, *Anomalospiza* does not mimic the song of its host species; no songs were recorded or heard like those of the local *Prinia* or *Cisticola* species.

Anomalospiza song has similarities both to certain ploceids (*Ploceus cucullatus*) and estrildids (*E. dybowskii*), and it is like the complex nonmimetic songs of certain species of *Vidua* (Village Indigobird, Payne 1973, 1985; Straw-tailed Whydah, Payne *et al.* 2002). The nonspecificity of song characters of *Anomalospiza* are consistent with more than one proposed systematic relationship, nevertheless the complex chirp is like that of certain *Vidua* species.

Conclusion

The bases upon which phylogenetic relationships were estimated for *Anomalospiza* in the past have been: (1) certain behaviours related to brood parasitism, (2) length of the outer primary, (3) mouth patterns of nestlings, (4) plumage colour, (5) seasonal plumage change, and (6) bill shape. The major systematic works that presented arguments for the relationship of *Anomalospiza* before Sorenson & Payne (2001) did so based on a subset of the above criteria (Chapin 1917, Delacour 1943, Bannerman 1949, Chapin 1954, Friedmann 1960). In fact the use of these few and discordant characters is responsible for the confusion that has existed over the relationships of this bird. None of these characters in isolation indicate the phylogenetic relationship of *Anomalospiza*, either because they are derived autapomorphic states within the genus (1, 6 and probably 3), or they do not consistently differ between Viduidae and Ploceidae (2, 4, 5).

Several traits differ between *Vidua* and *Anomalospiza*, and these relate to individualistic adaptations involved in brood parasitism or to other autapomorphisms. Among these are nestling mouth markings, begging and feeding behaviour, and egg colour (Payne 1998). Removal of host eggs by the female differs between the two genera, and the breeding displays and the double-scratch foraging technique of *Vidua* have not been seen in *Anomalospiza*. *Anomalospiza* has a distinctive bill and palate structure with a thickening of both the maxilla and adjacent horny palate that are adapted to the processing of hard seeds, and its sternal configuration also is uniquely derived.

Consistent with modern molecular and phylogenetic analyses, several characters support a close relationship between *Anomalospiza* and *Vidua*, and differ between Viduidae and Ploceidae. Most significantly, the skull pneumatization, the bony palate, the horny palate and several details of pterylosis of *Anomalospiza* are typically viduid. Both their morphological and behavioural traits and their molecular genetics indicate a sister relationship between *Anomalospiza* and *Vidua*.

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A description of copulation in the Kori Bustard *Ardeotis kori struthiunculus*

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Bustards are an Old World family with 25 species in 6 genera (Johnsgard 1991). Medium to large ground-dwelling birds, they inhabit the open plains and semi-desert regions of Africa, Australia and Eurasia. The International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Animals lists four species of bustard as Endangered, one as Vulnerable and an additional six as Near-Threatened, although some species have scarcely been studied and so their true conservation status is unknown. Agricultural changes, overgrazing, hunting, trapping, habitat loss, droughts and wars are the foremost threats facing all bustard species.

The Kori Bustard *Ardeotis kori* is a large polytypic bustard with two subspecies classified according to geographical distribution, size and plumage variations. One population, *A. k. struthiunculus,* resides in eastern Africa; the nominate race *A. k. kori* occurs in southern Africa (Johnsgard 1991). Kori Bustards are polygynous (Johnsgard 1991) and males gather singly or in loose lek-like formations to display to females during the breeding season. With neck inflated and wings drooping, a male struts around snapping his bill and producing a booming sound. If he is successful in attracting a female to his territory, copulation ensues, after which the male returns to his display grounds to attract another female. He plays no part in incubation nor in rearing the chicks.

The breeding biology of most bustards is poorly known and the events leading up to and including copulation are known for only a handful of species. The circumstances surrounding copulation have been described fully for wild populations